Some Observations on the Relation of the *Acaridæ* to the *Arachnida.* By HENRY M. BERNARD, M.A. (Communicated by A. D. MICHAEL, F.L.S.)

[Read 21st April, 1892.]

(PLATE XX.)

IN trying lately to deduce the Copepoda from some primitive form of *Apus*, which latter I had endeavoured to establish as the probable racial form of the majority of the modern Crustacea, I was driven to the conclusion that they could only be deduced from the larval forms of such animals. I was compelled to take this view because the organization of the Copepoda appeared to be much lower than that of any of the forms which I considered primitive. It occurred to me at the time that the relation of the Mites to the other Arachnids might perhaps be explained on the same principle. The principle is not that the animals degenerate, but that, in the struggle for existence, it has proved advantageous to many to remain at a larval stage, and thus minute enough to be inconspicuous both for purposes of escape and of attack. It may also be worth remarking that the more minute an animal is, the more abundant, relatively speaking, is the amount of organic matter at its disposal for purposes of nutrition.

It is true that, as the term is ordinarily used, this fixation of a larval stage would be called "degeneration;" but I think that the word "degeneration" is hardly applicable in this connection, and that it should be confined to those cases in which highly developed organs and functions, once acquired, have been lost owing to parasitism. It seems to me that no one who has studied the Mites, even in the most cursory manner, can believe that they are degenerated Arachnids in this latter sense, although they seem to have been generally called so. Many of them are active predatory creatures, with no such easy-going habits of life as would lead to degeneration; while among the Acarids themselves there are forms which have very clearly degenerated through parasitism, not from the Arachnidan, but from the Acaridan standard. I shall endeavour to show that this "degeneration" from the Arachnidan standpoint is almost purely quantitative, not qualitative.

If, then, they are not degenerated Arachnids (*i. e.* assuming them for the moment to be Arachnids), we must explain their minute size on some other principle, for, whether we adopt the Eurypterine or the more directly Annelidan origin of the Arachnida, we can hardly doubt that the primitive Arachnid was of much more imposing proportions than these microscopic creatures.

I propose in this paper to see whether it is possible to explain the origin of the Mites as I have endeavoured to explain that of the Copepoda *. I shall try to show that the Mites are not *degenerated* Arachnids, but Arachnids permanently fixed at a larval stage of development.

The establishment of this supposition appears, at the outset, to be by no means easy. Many of the Mites are very highly specialized, and reveal little as to their earlier morphology. Accident, however, threw in my way a form which seems to be rather primitive and to throw some light on the subject. I refer to the common *Tetranychus tiliarum* (Herm.), which I found swarming in countless thousands down a lime-tree last autumn, carefully keeping on the sheltered side of the tree.

This Mite is morphologically of importance, because its segmentation can be clearly made out, and it is on this naturally that one chiefly relies for the explanation of its morphology.

Fig. 1 (Pl. XX.) is a dorsal view of the animal, showing the arrangement of the hairs, the dorsal muscles, and the three segmental furrows and the relation of these furrows to the legs.

The muscles would, I think, clearly show that these two middle regions are true segments, even if the limbs did not make this evident. I feel justified, therefore, in diagrammatizing the segmentation of *Tetranychus* in the way show in fig. 2 B †.

We have the typical six segments of the Arachnidan cephalothorax (leaving out of consideration the possible vanished antennal segment), followed by *three* abdominal segments. The last or third segment, as we should expect, contains the anal aperture; just in front of the anal aperture is the genital aperture, whether on the first or second segment I cannot say; I have marked it between them.

When we compare this with the diagrammatic segmentation of an Arachnid (fig. 2 A), we find that the two agree very closely,

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* 'The Apodidæ.' Macmillan, 1892.

† We here assume that the mouth-parts of the Mites in general are purely Arachnidan, as they most clearly are in *Tetranychus*. We shall, however, return to this point.

with, however, this remarkable difference—some seven segments posterior to the genital aperture and in front of the anal aperture are missing.

Now when we remember that in the development of all articulate animals the rule is that new segments are added in front of the anal segment, we are justified in assuming, not only that the anal segments are homologous, but that the first eight segments in the Acarid are homologous with the first eight segments in the Araneid.

The segmentation of *Tetranychus* shows us very clearly, then, that it ceased to develop new segments as soon as eight segments had been formed, *i. e.* as soon as it had reached the typical position for the genital aperture, whereas, in the Araneids, some seven more segments are added between the genital aperture and the terminal or anal segment. This is the first and most important point, helping to bear out our suggestion that the Mites are Arachnids arrested in their development. I may add that the fact that no "waist" is formed in the Acarid between the 6th and 7th segment, as in the Araneid, is a point of no importance. A waist is simply a mechanical device to enable the animal to bend its body, which the Mites as a rule do not require; a few develop slight waists, but in another place, as will be mentioned below.

It is of course not necessary to suppose that all the Mites are to be deduced from the *same* Arachnida, or that all were arrested exactly at the same *stage* in their development. Some may have developed more abdominal segments than *Tetranychus*. On the other hand, it would be difficult for them to develop fewer. It would be necessary to develop some portion of the abdomen over and above the anal segment, as the genital glands typically arise in this part of the body, and without the power of reproduction the Mites of course could never have persisted as a distinct family.

Kramer has described the segmentation of a Mite (*Alycus roseus*?) with seven abdominal segments. Kramer counts nine by reckoning the last two thoracic segments as abdominal. This error arises from misunderstanding the arrangement of the limbs so common among the Mites, two pairs pointing forwards and two backwards, with a considerable space between the anterior and posterior pairs, which is simply an adaptive modification. The conclusion drawn from it by Kramer and others, that the line between these anterior and posterior pairs of limbs is the true waist or division between thorax and abdomen, cannot be maintained. The fact that *Alycus roseus* has a waist, as described by Kramer, may be due to the comparatively great length of its abdomen, all the larger species being capable of bending the body somewhat. It is, however, right to add that the claim that the line dividing the limbs into two pairs is the true demarcation between thorax and abdomen does not rest only on the arrangement of these limbs, but also on the fact that, in some Acarids, the mouth-parts are so specialized and altered from the primitive Arachnidan type that some would find in them 2nd maxillæ and an underlip presumably homologous with these same parts in the Hexapoda. I shall return to this presently.

My argument, however, does not rest only on the segmentation, although this is certainly the most important point. This arrested development theory throws some light on the nature and position of some of the internal organs.

Fig. 3 B (Pl. XX.) is adapted from Winkler's account of the anatomy of *Gamasus fucorum*. It shows the extraordinary position of the heart. If, however, we compare this with fig. 3 A, we have this position and shape very clearly explained. The *Gamasus* heart is, as it were, only the first chamber of the adult Arachnidan heart. The arrest of the further development of the abdomen naturally arrested the further growth of the heart.

This theory is of course different from that which sees progressive stages of degeneration in the hearts of the Phalangidæ, Chernetidæ, and Acaridæ. It is not impossible that some of the Acaridæ are to be deduced from larval Phalangidæ, but not as a result of degeneration, but as a fixation of larval forms. The heart of *Gamasus* is only quantitatively degenerated; relatively to the size of the animal it stands on the same level of organization as that of the adult Araneid.

Fig. 4 B is a diagram of the alimentary canal of a *Gamasus*, also after Winkler. If we compare this with the digestive tract of an adult Arachnid (e. g. *Mygale*, fig. 4 A), we see what is the part actually missing. It is again clearly the abdominal part, *i. e.* that portion of the mid-gut which lies between the thorax and the rectal vesicle. This offers further support to our theory that some seven segments between the 1st and 2nd abdominal and the anal segments were not developed. Here again we find the difference is more quantitative than qualitative.

The nervous system also offers slight confirmatory evidence. Fig. 5 (A, B) compares the nervous systems of an Arachnid (*Mygale*, A) and of a Mite (*Gamasus*, B). Only the great ventral ganglionic mass is developed in the latter. All its great diverging nerves correspond with those from the ventral ganglion of *Mygale*. When we reach the abdominal nerves, however, we find that in *Gamasus* they branch out direct from the sternal mass, while in the Araneid, in accordance with the form of the animal, they run together in a long strand (to swell in some cases, as in *Mygale*, into an abdominal ganglion) into the abdomen, and there branch out among the viscera.

The arguments here brought forward to show that the Acarids are larval Araneids receive some slight support from the fact that as a general rule in the Acarids the eggs are of an enormous size as compared with the parent animal. Although the Acarid stopped growing long before reaching the full number of segments of its adult original form, there was no reason why the eggs developing from the germinal epithelium should diminish in size in correspondence with the altered size of the parent. The size of the egg would of course gradually be fixed for each species by natural selection. It is, however, significant to find that, as a rule, the eggs of the Acaridæ are enormous, relatively, that is to say, to the size of the animals. This seems to indicate that the level of organization in the Mites has been well sustained, and that the alteration is almost entirely one of size.

These few comparisons between the internal structure of the Mites and that of other Arachnids (chiefly Araneids) lend considerable support to the evidence afforded by the segmentation, that the former are Araneids arrested in their development, *i. e.* that they are fixed larval forms.

The foregoing argument, it is clear, gains much in strength if it can be shown that *Tetranychus* can really claim to be a primitive form. I think that a study of the mouth-parts leaves little doubt on this point.

The mandibles have been somewhat telescoped into the body and are fused together, but their outlines are still clear (fig. 1). Although in *Tetranychus tiliarum* their distal joints have been modified into long retractile piercing-tubes, in another apparently allied species described by Flögel as parasitic on Spiders (in whose body its bite gives rise to a curious dendriform tissue) the mandibles are typical biting-jaws, like those of an ordinary Spider.

Again, the pedipalps are equally clearly Arachnidan. The basal parts are fused in the middle line and prolonged into a kind of chitinous beak, while their palps are 4-jointed, the penultimate joint being prolonged into a slightly curved hook which, with the terminal joint, forms a kind of chela. There is therefore in this case no difficulty whatever in homologizing the mouth-parts with those of an Araneid.

Following upon these mouth-appendages we have the typical four pairs of ambulatory legs of the thorax. These together make the typical six pairs of appendages of the Arachnids.

This certainly seems the simplest and most natural homology of the Acaridan limbs. It agrees best with all we know as to the development of the Acarids, which bears such striking resemblance to that of the Arachnids. It is necessary to emphasize this point, which we have hitherto assumed, because of the desire on the part of some to find other (? Hexapodan) homologies for the mouth-parts and limbs of the Acarids. Haller, for instance, claims a distinct 2nd pair of maxillæ and an underlip. The difficulties in the way of this interpretation of the Acaridan morphology are, it seems to me, overwhelming.

All other Arthropods, for instance, have antennæ, while the Acaridæ agree with the Arachnids in not having such appendages. Further, it is extremely doubtful whether the special structures which Haller claims as 2nd maxillæ and underlips can really be so interpreted. They appear to be secondary modifications in adaptation to the needs of the animal, and quite in accordance with the extraordinary specialization exhibited by so many of the Acaridæ in almost every part of the body. No trace of such extra mouth-parts can be found in such simple forms as *Tetranychus**. Winkler has described the underlip of *Gamasus*, and pointed out its very probable homology with the underlip of a Spider.

It seems to me, then, that this attempted change in the classification of the Acarids is in a high degree strained, in comparison with the usual classification which ranks them with the Arachnida, and which is based upon developmental history, upon general agreement in number and arrangement of appendages, and upon certain unmistakable likenesses in inner organization.

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* Mr. A. D. Michael, one of the first authorities on the Acarids, informs me that he certainly could not claim for the Mites any appendages homologous with the 2nd maxillæ and labium of the Hexapoda.

Of these last, perhaps the common possession of a tendinous endosternite is the most striking. This structure, whose probable origin I have described in another place *, only occurs, well developed †, in the Arachnida and in the archaic Crustacea, *Apus* and *Limulus*. We have not hesitated, therefore, in following the usual classification, and in claiming the Acarids as Arachnids throughout this paper.

I may sum up the arguments which lead me to believe that the Acaridæ are Araneids fixed at a larval stage of development because of the many advantages which animals of such small size have over larger ones, as follows :—

(1) On comparing the segmentation of a simple form of Acarid with that of an Araneid, seven abdominal segments in front of the anal segment are not developed, while all the developed segments in the Acarids are easily homologized with the similar number of anterior segments of the Araneid, segment with segment.

(2) We find, on comparing the alimentary canal of the Acarid with that of an Araneid, that it is clearly the abdominal part of the latter which is missing in the former.

(3) The heart of the Acarid (as exemplified by *Gamasus*) is clearly, both in shape and position, an Araneid heart arrested in its development ; the abdominal extension of it is wanting.

(4) The ventral ganglionic masses in both agree in almost every point, the only difference being due to the greater development of the abdomen in the Araneid.

(5) The size of the eggs of the Acaridæ is often out of all proportion to the size of the animals themselves ; this seems to show that, while the animal has diminished in size, the eggs have retained more nearly the size of those of the original adult forms.

(6) A further argument, based on the position of the tracheæ, will be adduced later on.

If the principle by which we have attempted to explain the origin of the Acaridæ holds good, it is probable that it has been of very general application in the development of the

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* 'The Apodidæ' (Macmillan, 1892), pp. 56, 57.

† There can be little doubt that a rudiment of it persists in *Astacus*.

Animal Kingdom. We have already elsewhere* endeavoured to explain by it the comparatively low state of organization and the diminutive size of many of the smaller forms of modern Crustacea. Indeed, we might institute many very interesting parallels between the smaller Crustacea and the Acaridæ; for instance, we have in the Ostracoda the abdomen with very few segments developed, and only occasionally a heart, the heart being, in all probability, the anterior end of the long dorsal vessels of their more developed ancestors—primitive Apodidæ or Trilobites.

It is further clear that the principle of the cessation of the development of segments can only be used for articulate animals whose method of development is still the primitive one for such animals, namely, that the segments are differentiated regularly in front of the anal segment. This method of regular axial development is often lost, owing to great specialization. In this case the segments are marked off upon the surface of a germinal disc. This modification would obviously allow of slight variations† in the inherited number of segments for each region of the body, variations which would hardly be possible so long as the axial method of development was retained. The Crustacea are a very interesting group in this respect; we have the primitive forms still developing from a *Nauplius* by the regular axial addition of new segments, while the higher forms, such as *Astacus*, mark off the segments almost simultaneously on a germinal disc.

The fact that in the Spiders the segments are marked off on the germ in no way interferes with our main argument, because the whole arrangement of the segmentations in the Spider-embryo shows very clearly that it is only a recent modification of the original method of axial development. The Spiders, indeed, like the higher Crustacea, form an excellent example of animals clearly derived from articulate ancestors in which, owing to high specialization, the old method of regular development of

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* 'The Apodidæ.' Macmillan, 1892.

† Professor Howes has kindly drawn my attention to the case of *Pipa*, which has only eight dorsal vertebræ, whereas all the other Anura have nine. The difference between the two methods of development is of great importance in the question of intercalation and excalation of segments; while it is obviously impossible that these processes could take place under the primitive axial method of development, they are quite possible under the later and more specialized method

new segments in front of the anal segment is in process of being lost, the segments being marked off nearly simultaneously on a germinal disc.

The absence of the seven abdominal Arachnidan segments from the Acaridæ is not a true case of excalation, because the method of development is still sufficiently axial to lead us to believe that when the Acaridæ were specialized this method of development was still the rule. These seven missing segments were therefore only excalated in the sense that the development of new segments ceased before reaching them.

This method of explaining the origin of the Acarids leads us almost necessarily to assume that the Acarids in each region were the fixed larval forms of the Araneids of that region—fixed, that is, at the time when the Araneids themselves had become specialized for their different habits of life.

It seems to me that the young of Araneids infesting trees or bushes would be very likely to find it advantageous to remain small and inconspicuous. The juices of the plant afford an abundant supply of nourishment always at hand, while their small size would render them comparatively safe, at least from the larger animals which prey on Spiders. Their small size, on the other hand, would make them very liable to be devoured by Ants, against whom each species has a special method of protection. *Tetranychus tiliarum* seems to live under a web which it spins; other Mites form galls, probably burrowing into the leaf originally to take refuge from the Ants. The Oribatidæ can afford to wander about freely, as, apparently after trying various disguises*, they have provided themselves with a thick chitinous shell, like a suit of armour. Others have even succeeded in making themselves the honoured guests, or valued slaves, of their foes †.

I hope in a subsequent communication to give an account of the minute anatomy of *Tetranychus tiliarum*.

Before concluding this attempt to show that the Acaridæ may be explained as Arachnids (probably Araneids) fixed in a larval condition, there are two points of considerable interest which cannot be ignored in any discussion as to their morphology.

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* See the beautiful disguises of some of the larvæ in Michael's 'Monograph of the Oribatidæ,' Ray Society.

† Michael, *vide* abstract in 'Nature,' vol. xlv. p. 164.

There is a point in the development of the Mites which has received considerable attention: that is the fact that the earliest larva has only three pairs of legs (*cf.* fig. 3 B); the fourth pair, which is usually the most posterior, is added as a further developmental process. At first sight this seems greatly to favour my theory of the undeveloped state of the hind body. But until more light has been thrown on Winkler's observation, that four pairs of limbs develop in the embryo, one pair being reabsorbed, only to be developed again in a later stage, I can hardly claim it as a support to my theory.

It is not easy to see the true bearing of Winkler's observation on the origin of the Acaridæ. The loss of a pair of legs is probably an adaptative modification to larval life *. As far as I can see, the temporary appearance of the fourth pair of legs in the embryo seems to show a tendency in the embryo to develop into the adult Araneid, as if the full number of abdominal segments were about to be developed. The sudden arrest of development, probably consequent on the exhaustion of the available supply of nutriment, leads to the reabsorption of the last pair of limbs, the power to redevelop them being only gradually regained after the larva has obtained for itself a fresh store of nourishment.

The tracheæ also demand some attention. Their position lends considerable support to our theory. The stigmata occur in many different parts of the body, but almost invariably on the cephalothorax, in some cases even so far forward as to be on the dorsal surface at the base of the mandibles. In the Arachnida (excluding the Acaridæ) the stigmata are, with one interesting exception, abdominal. The Solpugidæ have stigmata on the thorax. The Mites thus form a most interesting and important link between the Arachnids and the Antennate Tracheata. In the Araneids we have purely abdominal stigmata with tracheæ, both book-leaf and tubular. In the Solpugidæ we have tubular tracheæ alone, opening on both abdomen and thorax; and in the Mites we find the stigmata almost invariably on the thorax, the tracheæ being purely tubular. Now it is generally thought that the Solpugidæ are a somewhat primitive form of Arachnids; and if our theory is true, that the Acarids are larval Araneids, they would also be on the level of primitive forms in which we might naturally expect to find a more primitive tracheal system than that in the adult forms, especially as this branching off of the Acaridæ from the Araneidæ probably took place ages ago, when the latter were themselves first specialized for their peculiar manner of life.

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* A similar phenomenon occurs in the development of some Malacostraca, *cf.* Lang's 'Textbook of Comparative Anatomy,' pp. 410–411.

Hence we find that, as we go backwards from the specialized Araneids with their book-leaf tracheæ confined to the abdomen, we come to the Acarids with purely tubular tracheæ confined to the thorax, according to my theory necessarily, because so little of the abdomen is developed.

The presence of these tubular cephalothoracic tracheæ in the Arachnida is not only no difficulty, but is, on the contrary, most natural if the Arachnida are classed with the other Tracheata. The modern Hexapod has stigmata both on the thorax and abdomen, while the primitive forms had stigmata on all the thoracic segments, as is clearly seen in the embryos of many forms. The typical Myriapod has stigmata on every leg-bearing segment; and *Scolopendrella* is said to have them on the head; and lastly *Peripatus* has them all over the body. The Mites, then, in developing tracheæ in the anterior part of the cephalothorax have either retained the condition common to all primitive Tracheata, or else have returned to it, owing to their failure to develop a full number of abdominal segments.

This simple explanation of the facts is in striking contrast to the difficulties in the way of those who would deduce the Arachnidan tracheæ from the embedded gills of the abdominal legs of a *Limulus*-like ancestor. The only possible way to get over the difficulty is to assume that tracheæ have had four more or less independent origins. In the Hexapoda they have had one origin; in the Arachnida two independent origins—the abdominal book-leaf tracheæ from embedded leg-gills, the thoracic tubular tracheæ in some other way again, while the abdominal tubular tracheæ are modified book-leaf tracheæ. In one and the same group the same structure, viz. the tubular tracheæ, have thus had two independent origins! The more closely we examine this subject, in fact, the more improbable does the gill-origin of tracheæ appear. We have, for example, in *Ixodes ricinus* a pair of stigmata lying just behind the last pair of limbs. Until more is known of the segmentation of *Ixodes*, it is not easy to define the exact position of these stigmata; but they belong either to the last thoracic or to the first abdominal segment. However that may be, it seems clear from their position that they are closely related to the stigmata of the book-leaf tracheæ lying on the second abdominal segment of the Araneids. Pagenstecher's original drawing of the tracheæ opening through these stigmata is very instructive. We have a short thick trunk, ending in a close tuft of short tubules. They lie, not only in position on the body, but also in structure, halfway between the book-leaf tracheæ and the purely tubular thoracic tracheæ. Now, while it is impossible to assume that the *thoracic* tubular tracheæ came from embedded gills, it is not only not impossible, but highly probable, that both tubular and book-leaf tracheæ were derived from such tuft-like tracheæ opening as we have described on the first abdominal (or ? last thoracic) segment of *Ixodes*. The tubular tracheæ are tuft-tracheæ specialized for the respiration of the tissues directly. The book-leaf tracheæ are specialized for the oxygenation of a *blood-stream*, and thus of the tissues indirectly. A close parallel to this variation of tracheal arrangement in the Arachnids is afforded by the Myriapods, where, though tubular tracheæ are the rule, one group, the Scutigeridæ, have a kind of book-leaf system specialized for the aëration of the blood in the pericardium *.

If, therefore, the Acaridæ are true Arachnids, their tracheæ seriously complicate the position of those who would sever the Arachnida from the other Tracheata. Instead of one origin for these remarkable breathing-organs, they are forced, as above described, to assume *four* more or less distinct origins.

Although the important bearing of the Acaridæ on this question of the origin of the Arachnida has by no means been overlooked †, it has not received the attention it deserves. To me it appears strongly to confirm the old classification which placed the Arachnida with the other Tracheata.

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EXPLANATION OF PLATE XX.

N.B.—In all the drawings the line across the figure indicates the line of demarcation between thorax and abdomen.

Fig. 1. Outline of *Tetranychus tiliarum*, showing the three segmental furrows with arrangement of dorsal musculature; the dots show the position of the bristles. 1. The mandibles fused in the middle line and somewhat telescoped into the body. 2. The pedipalps also fused in the middle line. 3, 4, 5, 6. The four pairs of ambulatory limbs belonging to the four thoracic segments. I, II, III. The three abdominal segments, with the genital and anal apertures.

Fig. 2. A. Diagrammatic segmentation of an Araneid. 1–6. The six segments of the cephalothorax, each provided with a pair of limbs. I–X. The segments of the abdomen, showing the positions of the genital and anal apertures.

B. Segmentation of *Tetranychus* (*cf.* fig. 1) for comparison with A. 1–6. The cephalothoracic segments homologous with 1–6 in A. I, II, III. The abdominal segments, of which I and II are homologous with I and II in A, and III homologous with X, showing that seven segments are undeveloped.

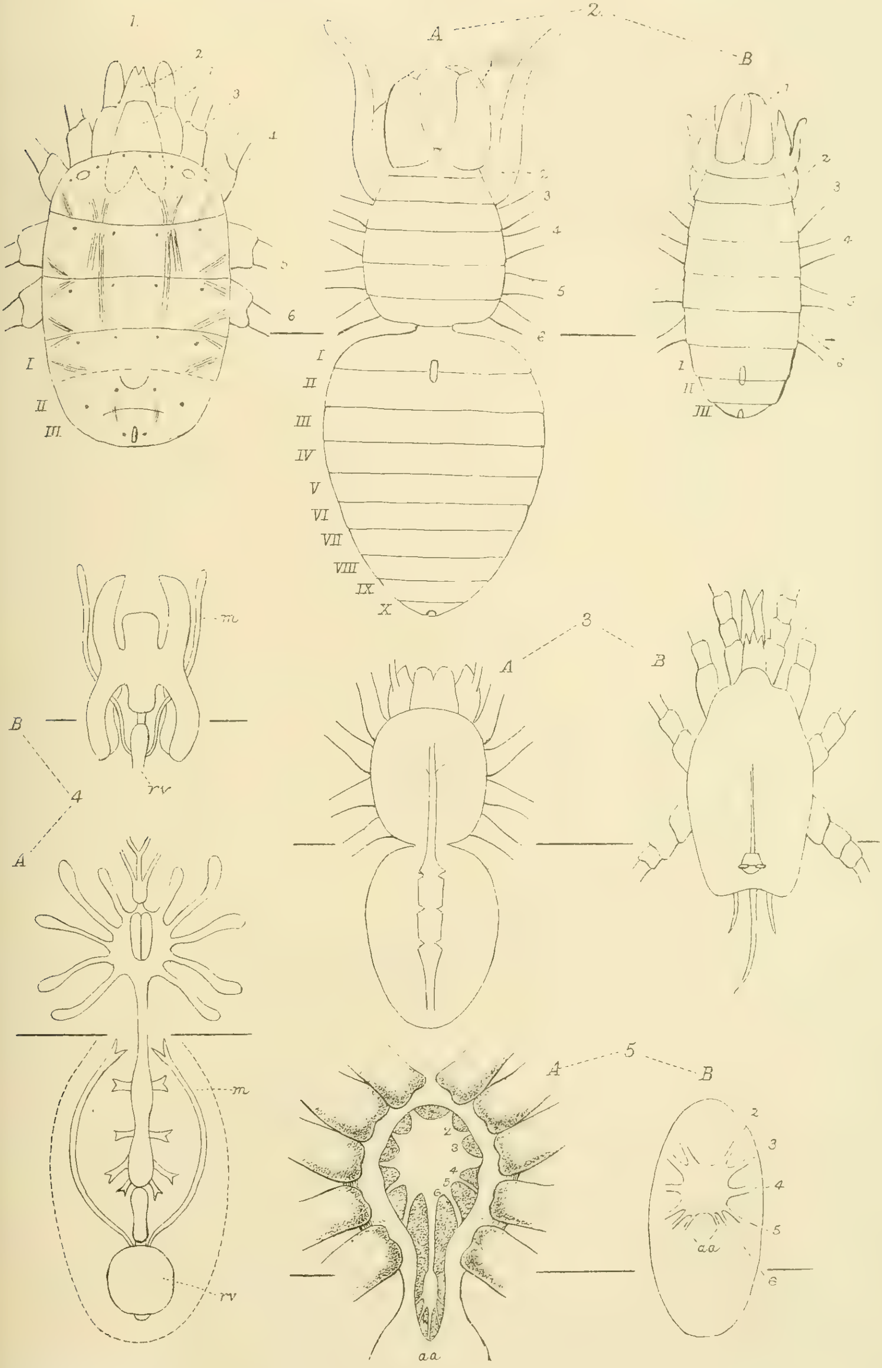
Fig. 3. A. Diagram of heart of an Araneid lying entirely in the abdomen.

B. Diagram of 3-legged larva of *Gamasus fucorum* (adapted from Winkler), showing position and stage of development of the heart for comparison with A.

Fig. 4 (from Lang's 'Text-book of Comparative Anatomy'). A. Alimentary canal of an Araneid (*Mygale*): *m*, Malpighian tubule; *rv*, rectal vesicle. B. The same of *Gamasus*. A comparison of the two shows that it is the abdominal portion of the adult Araneid alimentary canal which is not developed in the Mite.

Fig. 5. A. Ventral ganglion of an Araneid (*Mygale*, adapted from Lang's 'Text-book of Comparative Anatomy'). 2–6. The five posterior cephalothoracic appendages, each supplied with a nerve. *a*, *a*. The visceral nerves radiating from an abdominal ganglion.

B. The same of *Gamasus* (after Winkler). 2–6. Nerves branching to 2nd to 6th appendages. *a*, *a*. The ventral nerves branching directly from the ventral ganglion.



H. Bernard del.
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MORPHOLOGY OF THE ACARIDÆ.